AN UNUSUAL FLIGHT MECHANISM IN THE PTEROSAURIA

by GRANT A. HAZLEHURST *and* JEREMY M. V. RAYNER

ABSTRACT. The motion at the shoulder joint of the Cretaceous pterodactyloid pterosaur *Santanadactylus brasilensis* is investigated. Shoulder movement is important because it determines the orientation and amplitude of the wing stroke during flapping flight. In previously studied pterosaurs, the principal shoulder motion is in the transverse vertical plane with, in at least one species, a degree of rotation about an axis along the length of the wing. However, in *Santanadactylus brasilensis*, evidence from direct articulation of the bones and from morphological analogues indicates that shoulder movement was restricted to rotation of the humerus about its long axis. The nature of the flight stroke produced by this motion depends upon the position of the humerus relative to the body. At maximum extension, humeral rotation was converted into rotation of the wing about the axis joining shoulder and wing tip, while if the humerus was held as close as possible to the body humeral rotation would give rise to a small amount of vertical wing movement, as well as rotation about the axis joining the shoulder to wing tip. The former wing motion might be used in braking, while the latter wing motion could have produced useful aerodynamic force for maintaining horizontal flight. Before this unusual shoulder motion could have evolved, flapping flight must have reduced in importance, and wing rotation may have arisen in response to pressures to minimize wing inertia.

THE pterosaurs were a group of Mesozoic flying reptiles, possessing a wing supported along its leading edge by the forelimb, and in particular by the enormously elongated fourth digit. The smaller species at least were capable of flapping flight (Padian 1983*a*). Perhaps the most significant supporting evidence is the convergence between the pectoral girdles of pterosaurs and of birds, indicating the presence in pterosaurs of enlarged pectoral muscles necessary for flapping flight. Other lines of evidence include the morphological specialization of the forelimb and the stiffening of the flight surface. However, like many of the larger species of birds, the larger pterodactyloids probably spent an appreciable part of their flying time soaring, and glide polars calculated for larger pterosaurs indicate that they were proficient soarers (Bramwell 1971; Heptonstall 1971; Bramwell and Whitfield 1974; Brower 1983). There are also energetic pressures for larger species to soar: as size increases the energy required to fly forms a greater proportion of the metabolic energy available, and ultimately exceeds it (Rayner 1988*a*).

Motion at the shoulder joint has an important role in determining the movement of the forelimb, and hence of the wing. The shoulder joint consists of the proximal articular surface of the humerus and the glenoid, a modified portion of the scapula and coracoid. In birds and bats, the humeral head rotates in a near vertical arc in the glenoid to produce the typical cruising flight stroke. It is possible to infer the motion at the pterosaurian shoulder joint from the fossils in two separate ways, articulation of uncompressed material, and identifying the function of morphological analogues in other vertebrates; an analogous system with similar morphology will have a similar motion, particularly if the morphology is specialized or in some other way unusual.

There are several criteria by which articulation of uncompressed material may be used to define the motion possible: either the movement with least resistance between the bones (Jenkins 1971), or the path along which the majority of the joint surface is utilized (Kemp 1980), is determined. This approach works best when animals have fully calcified epiphyses. It also requires that soft tissue, in particular cartilage on the articular surfaces, did not modify the motion appreciably. This is more likely to be a valid assumption when there was little cartilage present. Evidence for the absence of

a thick layer of cartilage upon an articulation includes smooth and unpitted joint surfaces, and a tight fit between the articular surfaces. The application of this method to the platypus (*Ornithorhynchus anatinus*) illustrates how this approach can produce valid conclusions. Howell (1937) inferred the motion at the shoulder joint by articulation of the humerus and the glenoid, and inferred that the only feasible motion was rotational. It was not until much later that the actual motion was observed by cineradiography (Pridmore 1985), confirming Howell's inference.

Previous studies of the motion at the pterosaurian shoulder joint have mostly been based upon the first approach, and have reached the conclusion that the principal flight motion was in a vertical plane, and produced wing kinematics similar to those seen in flying birds and bats. Hankin and Watson (1914), using Cretaceous pterodactyloid material from the Cambridge Greensand in the Natural History Museum, described the pterosaurian shoulder articulation as forming a hinge joint, which only permitted vertical motion. They considered that the motion at the shoulder joint was rather more limited than that in birds and bats, with no other movement of the humerus possible. Bramwell and Whitfield (1974), on the basis of analysis of similar pterodactyloid material, found that the principal motion was in a vertical plane. The extremes of the motion occurred when the humerus reached angles of 25° below the horizontal, and 70° above. They identified a locking mechanism in the joint which could have maintained the wing in a soaring position with minimum muscular effort; this consisted of an interlocking ridge on the humeral articulation and a groove upon the glenoid. However, this interpretation is flawed (Padian 1985). The groove along the glenoid is not a specialized feature of certain giant pterodactyloids, but is present in all pterosaurs, and represents the line of fusion between the scapula and coracoid. The humeral ridge is unlikely to have come into contact with the groove because it does not form part of the articular surface, but was the boundary between humeral head and shaft.

Padian (1983a, 1983b) inferred the shoulder motion in the Jurassic 'rhamphorhynchoid' *Dimorphodon*. Direct articulation of humerus and glenoid revealed that movement at the shoulder joint was restricted to two motions: a vertical arc of 90°, or an arc inclined to the vertical with a forward rotation of the humerus during the downstroke. By analogy with birds and bats (e.g. Rayner 1988a) a more vertical flight stroke was used at higher flight speeds, and an inclined flight stroke at lower speeds and when accelerating. The rotational component of the flight stroke was further demonstrated by similarities in humeral morphology with tetrapods in which humeral rotation plays a significant role (e.g. the echidna, sea turtles and plesiosaurs). The projection of the deltopectoral crest from the shaft, which is more pronounced in pterosaurs than in birds, means that contraction of the pectoral muscle would generate a suitable turning moment for rotating the humerus.

A shoulder motion somewhat different from those previously described has been recognized for the Cretaceous pterodactyloid *Anhanguera santanae* (Wellnhofer 1991); humeral movement below the horizontal was impossible, while movement to a 45° angle above the horizontal and rotation about the humeral long axis was possible.

MATERIALS AND METHODS

The paratype of the large Cretaceous pterodactyloid *Santanadactylus brasilensis* consists of most of the scapulocoracoid and humerus (Geological Institute of the University of Amsterdam, M4894). The glenoid and proximal articular surface of the humerus are preserved complete, uncrushed, and unabraded. This study is based on a cast of this specimen (Text-fig. 1), which was fully described by de Buisonjé (1980). The glenoid consists of a notch at the junction of scapula and coracoid. The notch is saddle-shaped, i.e. it has a convex profile and a concave profile perpendicular to one another. The concave profile is delimited by lips on the scapula and the coracoid portion of the glenoid. The humeral head, when viewed dorsally (i.e. from above when the humerus is held out), has a slightly convex surface. When the proximal articulation is viewed end on, it has a reniform outline. The dorsal surface is convex, and the ventral surface is concave. Pitting can be seen on the
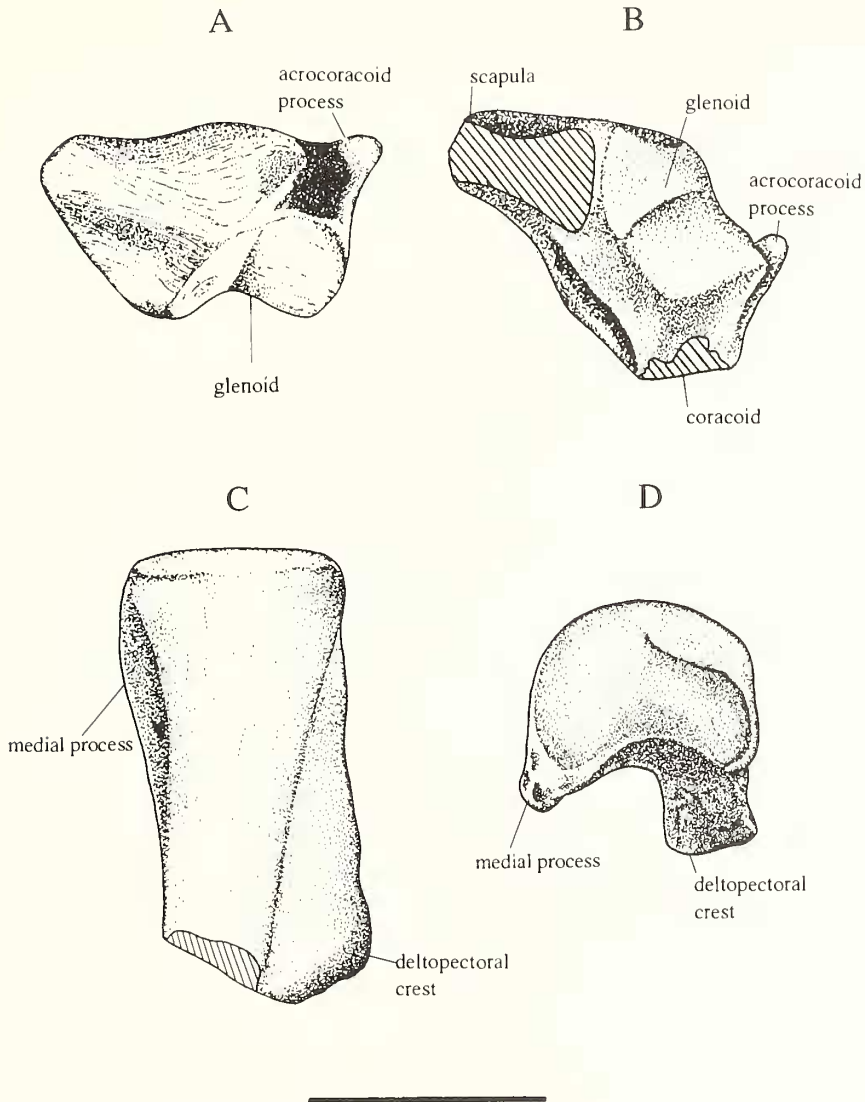
TEXT-FIG. 1. *Santanadactylus brasilensis.* A–B, glenoid; positioned at the junction of scapula and coracoid, dorsal and lateral views. C–D, humerus only the proximal 40% of the shaft is preserved, dorsal and anterior views. Scale bar = 50 mm.

ventral surface of the deltopectoral crest, and represents the area where the pectoral muscle responsible for the downstroke was attached to the humerus.

Owing to the limited extent of the preserved skeleton, *Santanadactylus brasilensis* cannot be assigned to any family (Wellnhofer 1991). However, the shoulder joint is morphologically similar to that of other Santana Formation pterosaurs (*Anhanguera santanae* and *Santanadactylus pricei*), as well as to certain specimens from the Cambridge Greensand (discussed in greater detail below).

In the original specimen the humerus and scapulocoracoid are connected by a ribbon of sediment, which prevents direct articulation. The image of this ribbon of sediment was removed from the cast to permit articulation.

RESULTS

Direct articulation

The results of direct articulation were unambiguous. An appreciable degree of rotational motion in the vertical plane was expected (i.e. movement in a vertical arc with the shoulder as the pivot), as this corresponds to dorso-ventral flapping of the wing. However, appreciable vertical movement was not possible. Downward movement of the humerus from the horizontal leads to almost instantaneous disarticulation. A greater amount of motion is possible above the horizontal, but within approximately 15° the articulation is reduced to point contact between the humeral head and the coracoid part of the glenoid.

The joint is essentially restricted to rotational motion about the humeral long axis (Text-fig. 2). The convex coracoid lip acts as a pivot about which the humerus rotates. The coracoid and scapula lips of the glenoid restrict the motion of the humerus. The movement is not simply a rotation about the humeral long axis, but also involves the humeral head sliding through the glenoid. A similar rotational and sliding movement has been described in the shoulder articulation of the platypus (Howell 1937).

Although it seems clear that motion at the shoulder joint was rotational, the actual amount of movement possible can only be defined subjectively, because the amount of rotation and sliding will
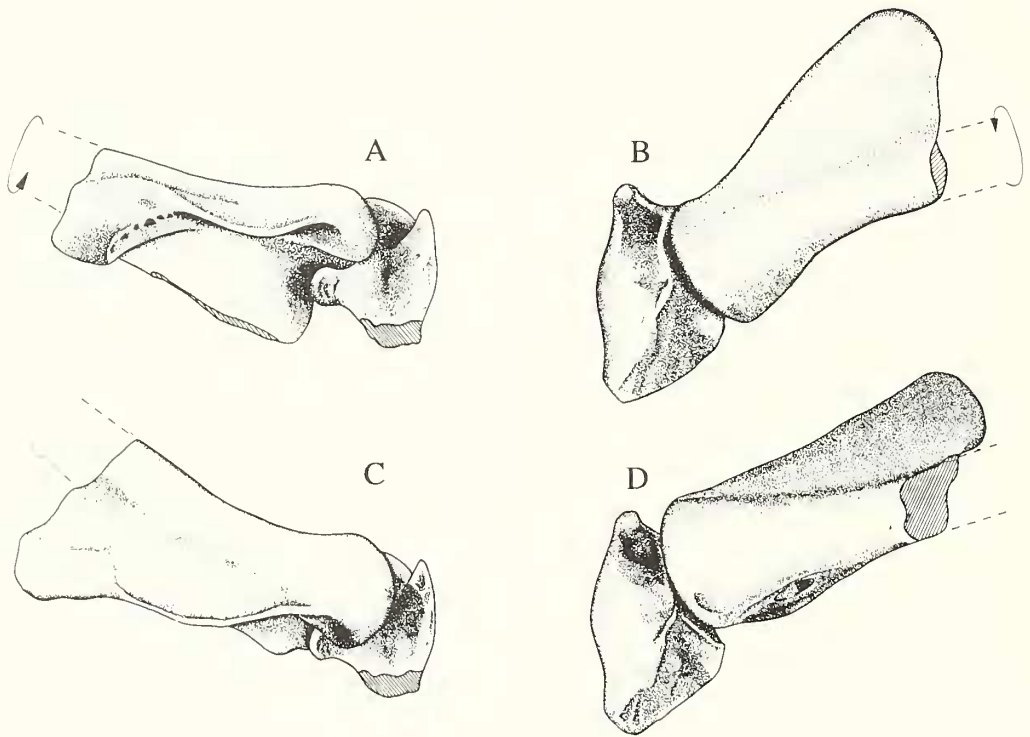
TEXT-FIG. 2. The rotational movement possible at the shoulder joint. Rotation takes place about the humeral long axis. A–B, humerus is in a supinated position; the arrows show the sense of rotation towards a pronated position, anterior and dorsal views. C–D, humerus in a pronated position, anterior and dorsal views. Scale bar = 50 mm.

be restricted by soft tissues. If it is assumed that sliding occurs to the point at which there is only 50 per cent contact between humeral head and glenoid, the humerus can rotate through an angle of 70° about its long axis. During this rotation the deltopectoral crest moves from a position just below the horizontal down to one approaching the vertical. Although it is the principal motion, rotation is associated with a limited amount of movement in the vertical plane. During a 70° rotation forward the humerus moves dorsally by approximately 15°, and posteriorly by 5–10°.

Morphological analogues

An obvious place to look for analogues to the pterosaur shoulder joint is the extant flying vertebrates. However, despite broad similarities between the bird and pterosaur pectoral girdle, humeral morphology of birds and bats is very different from that of any pterosaur (Text-fig. 3). In bats the humeral head is spherical, while in birds it is an elongated hemisphere. There is little variation in the articular morphology in either group. Owen (1861) compared pterosaur and avian humeral morphologies. The convex structures of birds and bats are very different from the more complex articular morphologies of the pterosaurs, and also seem to allow a greater range of motion (Hankin and Watson 1914; Padian 1983b).

Similar humeral morphologies might also be expected in the relatives of pterosaurs: the Archosauria. Humeral heads of a dinosaur, crocodile and bird are illustrated in Text-figure 3. There is no clear similarity in humeral head between the pterosaurs and any archosaur group, in all of which the humeral head is either elliptical or cylindrical. The only group of reptiles with curved humeral heads approaching the morphology of the pterosaurs are the cynodonts. Seeley (1901) interpreted this similarity as being the result of inheritance from a common ancestor, but we consider this interpretation unlikely, because similar humeral heads do not occur in non-pterosaurian archosaurs. Moreover, the resemblance between pterosaurs and cynodonts is not complete: the curvature of the humeral head of cynodonts is rather less than that of any pterosaur. The glenoid of cynodonts is highly convex, so that when the humerus and glenoid are brought into contact they only touch across a small area, and as a result a large amount of movement is feasible (Jenkins 1971; Kemp 1980). In contrast, when the humerus and glenoid of *Santanadactylus brasilensis* are articulated, the area of contact is much greater, and the range of movement is much less.

The closest structural analogue to the shoulder joint of *Santanadactylus brasilensis* is found in certain extant mammals (Text-fig. 4). Reniform humeral heads and notch-shaped glenoids have evolved in the monotremes and in the moles, which are the 'humeral-rotation' diggers of Hildebrand (1985); of these mammals the echidna shows the greatest degree of similarity. In moles the humerus has two proximal articular surfaces. The true humeral head is positioned on one side of the shaft, and a second articular surface representing the greater tuberosity is positioned on the proximal end of the bone (Reed 1951). This second articular surface bears a close resemblance to the humeral head of *Santanadactylus*. It articulates not with the glenoid, but with the clavicle, at a saddle-shaped notch similar to the pterosaurian glenoid.
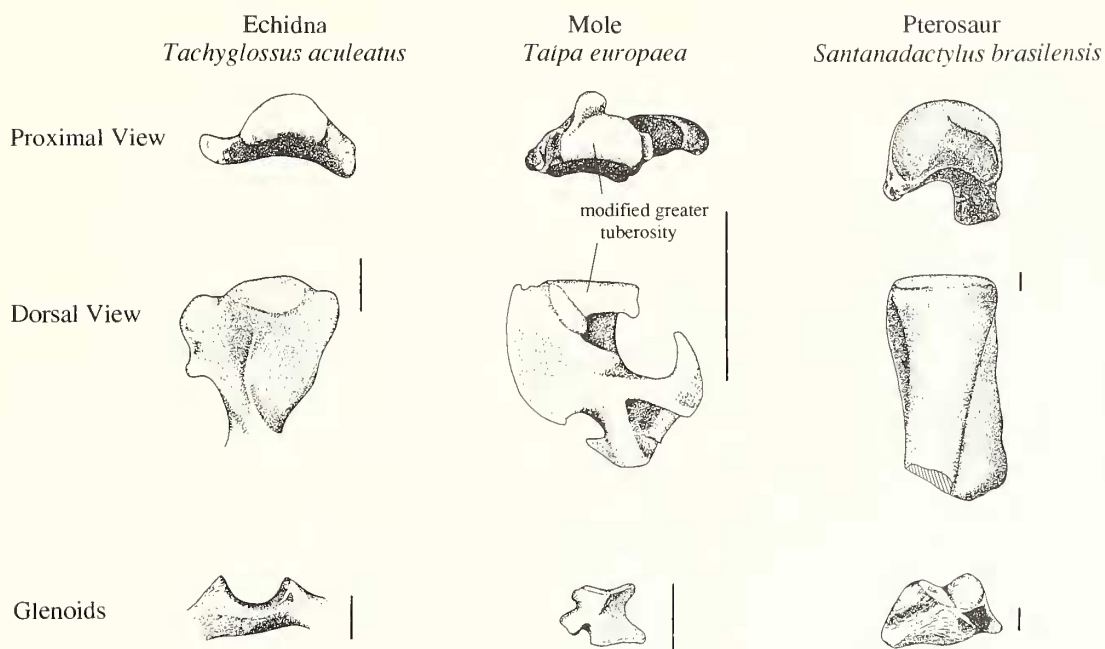
In monotremes (Reed 1951; Yalden 1966), and moles (Jenkins 1970; Pridmore 1985) the principal motion of the humerus is rotation about its long axis. These animals typically have a semi-erect stance in which the humerus lies parallel to the ground, and transverse to the body. Rotation of the humerus is translated into forward locomotion when the elbow joint is held rigid, approximately at a right angle. The adaptation has evolved in association with digging, as it also permits strong lateral strokes of the forelimbs. Padian (1983a) has previously recognized that the 'concaveness' of the pterosaurian humeral head is similar to that of the echidna and mole. The more marked structural resemblance of the humeral head in *Santanadactylus* with these mammals is supporting evidence for our argument that the principal motion was rotation of the humerus.

MORPHOLOGICAL VARIATION OF THE PTEROSAURIAN HUMERAL HEAD

Shoulder motion of *Santanadactylus brasilensis* seems to have been quite different from that
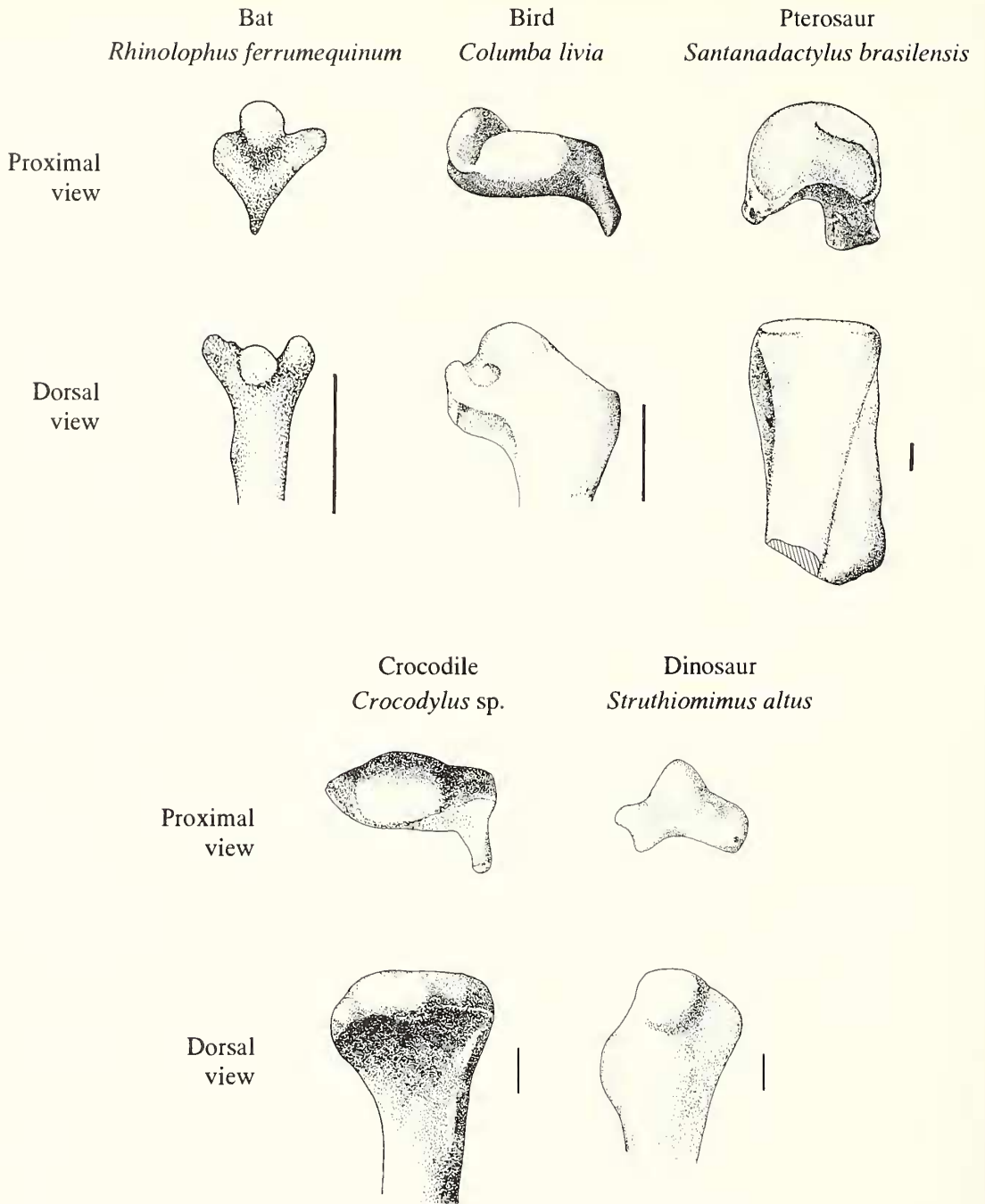
TEXT-FIG. 3. Comparison of the proximal humeral articulation among flying vertebrates and archosaurs. The deltopectoral crests are situated to the right of the shafts. The humeral head of bats is a subspherical structure, the humeral head of birds has an elliptical form, while the humeral head of *Santanadactylus brasilensis* is reniform. The humeral head of the crocodile (Owen 1861) is elliptical, similar to that of birds, and the ornithomimid dinosaur illustrated (from Osborn 1917) has a subspherical humeral head. Scale bars = 10 mm.

Echidna	Mole	Pterosaur
Tachyglossus aculeatus	*Taipa europaea*	*Santanadactylus brasilensis*

Proximal View

modified greater
tuberosity

Dorsal View

Glenoids

TEXT-FIG. 4. Comparison of the proximal humeral articulation among the echidna, mole and *Santanadactylus brasilensis*. The deltopectoral crests are situated to the right of the shafts. All three groups possess reniform humeral heads. The glenoids are illustrated along the bottom row, opening uppermost. In the mole, the principal articular surface is the modified greater tuberosity, which articulates with the modified clavicle. Scale bars = 10 mm.

described for *Dimorphodon* (Padian 1983a, 1983b) and the Cambridge Greensand species (Hankin and Watson 1914; Bramwell and Whitfield 1974). There are similarities between the shoulder motion of *Santanadactylus brasilensis* and *Anhanguera santanae*; in both, ventral movement of the humerus was impossible, and in both rotation of the humerus about its long axis was feasible. However the resemblance is not complete: we consider dorsal movement of the humerus in *Santanadactylus brasilensis* impossible, whereas Wellnhofer (1991) recognized that dorsal movement through at least 45° was possible for *Anhanguera santanae*.

The difference in humeral motion between pterosaurs must result from differences in the architecture of the shoulder articulation. Within the pterosaurs the glenoid seems to have been morphologically conservative, whereas the humeral head exhibits a greater amount of variation (Text-fig. 5). The majority of species, including many pterodactyloids and all rhamphorhynchoids, have similar humeral morphology, but a different pattern is found in certain Cretaceous pterodactyloids, which probably represent a derived condition. In the great majority of pterosaurs (including *Dimorphodon*) the humeral head when viewed dorsally is concave, and can be described as saddle-shaped. In contrast, in *Santanadactylus brasilensis* the humeral head is slightly convex when viewed dorsally. In all pterosaurs, the humeral head when viewed end on has a curved shape, with a convex dorsal surface and a concave ventral surface. However, in *Santanadactylus brasilensis* the humeral head has a greater degree of curvature, giving it a more reniform outline than the 'banana' outline of other species. Differences are not restricted to the articular surface; associated with the more derived humeral head is the warped delto-pectoral crest described by Bennett (1989).

The morphological variation of the humeral head is illustrated in Text-figure 6. Measurements were made on specimens considered not to be appreciably distorted by compression. The ordinate is the ratio of humeral head depth (b) to width (a), and the abscissa is the ratio of humeral head concavity or convexity (c) to width (a). The width of the humeral head is measured between the
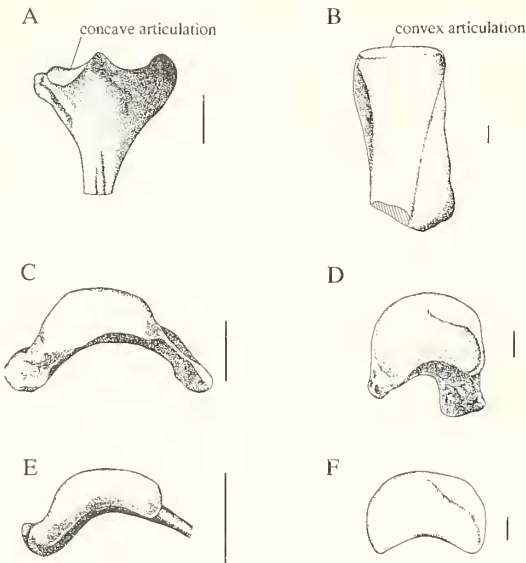
TEXT-FIG. 5. Variation in humeral morphologies within the pterosaurs. A–B, dorsal views of humeri. C–F, anterior views of proximal humeral articulations. A, *Dorygnathus banthensis* DSB 759h. B, D, *Santanadactylus brasilensis*. C, *Ornithocheirus clifti*, BMNH 2353. E, '*Pterodactylus*' sp., BMNH R1776. F, *Ornithocheirus simus*, BMNH 35830. Scale bars = 10 mm.

anterior and posterior extremities of the articular surface; depth is measured at the mid-point of the humeral head. Concavity or convexity is measured when the shaft is held horizontal, so that the humeral head can be viewed in dorsal aspect, and is measured from the centre of the articular surface to the line joining the extreme anterior and posterior points of the articular surface. If the outline of the articular surface when viewed from above is concave, c is negative, and, if it is convex, c is positive.

Rhamphorhynchoids (*sensu lato*) form a discrete cluster with relatively broad and concave humeral heads when viewed from a dorsal aspect. The pterodactyloids occupy a larger region of the plot, and fall into two groups. Pterodactyloid group A resembles the rhamphorhynchoids. This group includes specimens from the Cambridge Greensand (e.g. *Ornithocheirus clifti* and *Pterodactylus sedgwickii*) and *Quetzalcoatlus* (although the position of *Quetzalcoatlus* cannot be defined with certainty because the measurements were made from a photograph in Lawson 1975). Pterodactyloid group B had relatively deeper and convex humeral heads when viewed from the dorsal surface. This group contains *Santanadactylus* species, *Anhanguera santanae* and certain specimens of *Ornithocheirus* from the Cambridge Greensand, although other examples of this genus fall into pterodactyloid group A. The range in morphology within *Ornithocheirus* probably reflects the fact that the genus contains several distinct taxa (Hooley 1914). The morphological similarity of the *Santanadactylus brasilensis* humerus to some Cambridge Greensand material is not surprising in the light of the taxonomic similarities between the two faunas (Unwin 1988). Species in group B, including *Santanadactylus brasilensis*, are expected to have had similar shoulder movements. All members of the group could rotate the humerus about its long axis, but could not move it ventrally. Dorsal movement within the group is probably more variable. *Anhanguera santanae* could lift its humerus (Wellnhofer 1991), but *Santanadactylus brasilensis* could not, and it is difficult to explain this difference when the shoulder architectures are so similar. However, it is clear that in both *Anhanguera santanae* and *Santanadactylus brasilensis* a full vertical flapping motion similar to the flight motion of extant birds and bats (as well as to rhamphorhynchoids and to pterodactyloids in group A) was not possible, and instead wing movements used for flight must have involved less vertical movement and relatively more rotation.

Bennett (1989) has discussed the taxonomic significance of the humerus in the pterodactyloids. The humerus in Pteranodontidae can be characterized by a number of synapomorphies, which include a warped delto-pectoral crest positioned obliquely to the long axis of the shaft and a

pneumatic foramen on the dorsal surface near the medial crest. These features seem to be present for all members of pterodactyloid group B. Thus pterodactyloid group B may represent the Pteranodontidae, while group A may represent other groups of pterodactyloids.

THE FLIGHT MECHANISM OF *SANTANADACTYLUS BRASILENSIS*

The large size of *Santanadactylus brasilensis* (wingspan in the region of 4·7 m (Wellnhofer 1985), and body mass of 3·9–7·3 kg, assuming geometric similarity with the *Pteranodon* reconstruction of Bramwell and Whitfield (1974)) suggests that it would need to have spent most of its flying time soaring rather than flapping, because for large pterosaurs flapping flight would have been prohibitively energetically expensive (Bramwell and Whitfield 1974; Brower 1983). However, even the largest extant soaring animals need to flap their wings occasionally, during take-off or while manoeuvring. It would therefore be expected that *Santanadactylus brasilensis* would have also retained a limited capability to use its wings for powered flight. Flapping movements similar to those of birds and bats were impossible in *Santanadactylus brasilensis*, and its flight stroke must therefore have been rather unusual.

How humeral rotation was converted into a flight motion depends upon the orientation of the humerus relative to the rest of the wing and body, which in turn is determined by the orientation of the glenoid. Wellnhofer (1991), using exceptionally preserved material of the pectoral girdle, established that the long axis of the humerus of *Anhanguera santanae* was directed 15° behind the transverse axis of the body when the wing was held fully open (Text-fig. 7A) and could be swung back so the long axis was directed at most up to 25° behind the transverse axis (Text-fig. 7C); this gave the humerus only a limited anterior–posterior excursion. A similar humeral position and degree of anterior–posterior movement is expected in *Santanadactylus brasilensis*.

Assuming that the only motion of the humerus possible is rotation about its long axis, the vertical excursion of the wing tip h can be expressed in terms of θ, the amount of rotation of the humerus about its long axis, as

$$h = 2l \sin \phi \sin (\theta/2),$$

and the amplitude of the wingbeat is

$$\Phi = 2 \tan^{-1} (h/2l) = 2 \tan^{-1} \{\sin \phi \sin (\theta/2)\};$$

angular rotation (pronation) of the wing surface, measured perpendicular to the wing-finger, is Ω, given by

$$\sin (\Omega/2) = h/(2l \tan \phi) = \cos \phi \sin (\theta/2);$$

l is the distance from wing root (the shoulder) to tip, and ϕ is the angle between the long axis of the humerus and the line joining wing root to wing tip. For the calculations we used Wellnhofer's reconstruction of the wing of *Santanadactylus pricei* (Wellnhofer 1991, fig. 35); $l = 1 \cdot 62$ m.

When the humerus was held at maximum extension, at 15° behind the transverse axis of the body, ϕ is 0° (i.e. the wing tip lies along the extension of the humeral long axis, although the radius, ulna and hand bones lie in front of this axis). Thus for a humeral rotation θ of 70°, rotation (Ω) of the wing tip and flight surface is also 70°, there is no vertical excursion ($h = 0$, $\Phi = 0$); the only movement of the flight surface is a pitch oscillation (Text-fig. 7B), which could possibly produce useful aerodynamic force. Clues to how it could have been used can be gained from situations where flying vertebrates use similar wing kinematics.

(i) Similar pitch oscillation has been observed in Wilson's storm petrel (*Oceanites oceanicus*) in 'hovering' close to water, with the feet trailing in the water (Withers 1979); there was virtually no movement of the wing in a horizontal or vertical plane, but only a very rapid pitch oscillation, generated by rotation of the humerus about its long axis. This was not considered to be a form of soaring because it occurred in conditions where there is very little air movement. It it not clear how the aerodynamic forces were being generated in this situation. The use of pitch oscillations for
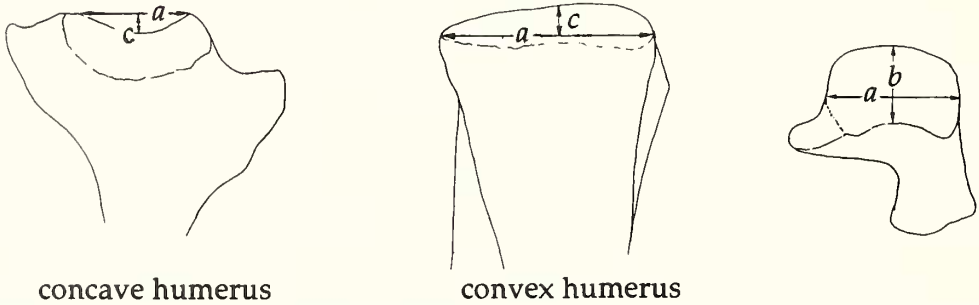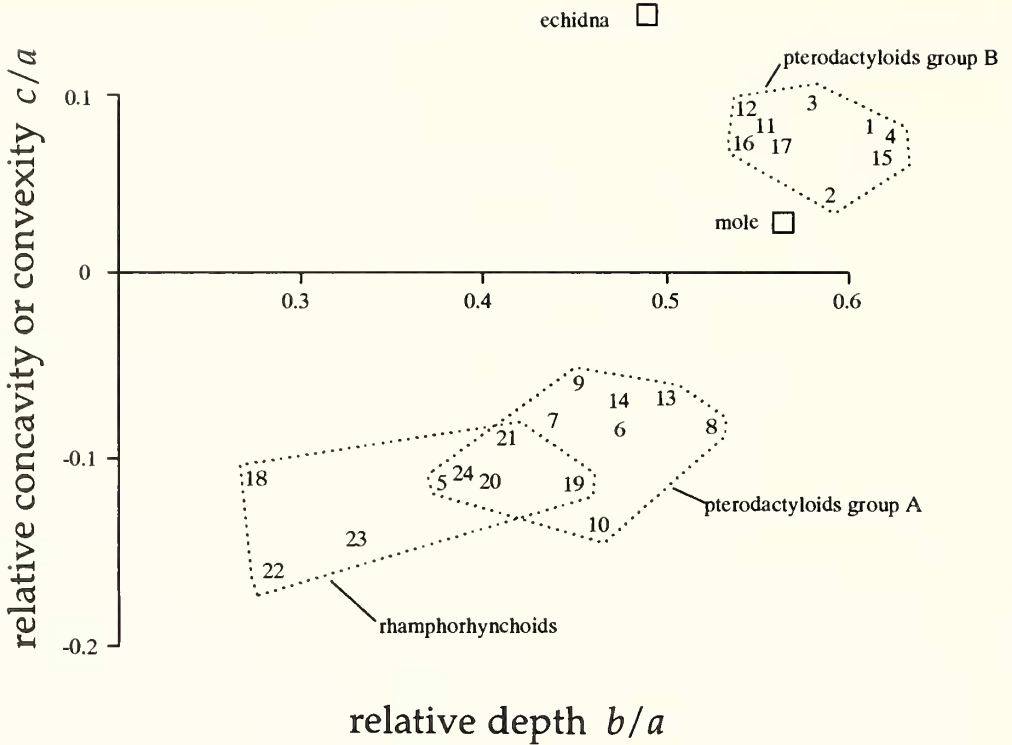
TEXT-FIG. 6. Range of proximal humeral articular morphologies within the Pterosauria. The ordinate is the ratio between humeral depth (*b*) and width (*a*), measured when the humeral head is viewed from the anterior aspect; the abscissa is the ratio between humeral head convexity or concavity (*c*) to width (*a*) when the humerus is viewed from the dorsal aspect: a convex humeral head is given a positive value, and a concave humeral head is given a negative value. Symbols: 1, *Santanadactylus brasilensis* (this paper); 2, *Santanadactylus araripensis*, BSP 1982 I 89; 3, *Santanadactylus* cf. *S. araripensis*, BSP 1982 I 92; 4, *Anhanguera santanae*, AMNH 22555; 5, '*Ornithocheirus clifti*' (Owen 1846, figs 5–6); 6, Cretaceous pterosaur (Gilmore 1928); 7, *Quetzalcoatlus northropi* (Lawson 1975); 8, '*Pterodactylus*' *nanseli*, BMNH 41970; 9, '*Pterodactylus*' *sedgwicki*, BMNH 35233; 10, '*Ornithocheirus*' *clifti*, BMNH 2353; 11, '*Ornithocheirus*' *sinus*, BMNH 35830, 12, *Ornithocheirus* sp., BMNH 35408; 13, *Ornithocheirus* sp., BMNH R558; 14, *Ornithocheirus hlavatschi*, BMNH R1031; 15, *Ornithocheirus* sp., BMNH R1908; 16, *Ornithocheirus* sp., BMNH 2299; 17, Cretaceous pterosaur (Bennett 1989); 18, *Dimorphodon macronyx* (Padian 1983*a*); 19, *Dimorphodon macronyx*, BMNH 41348; 20, *Dimorphodon macronyx*, BMNH 43974; 21, *Dimorphodon macronyx*, BMNH R1598; 22, *Dorygnathus*

A

B

C

D
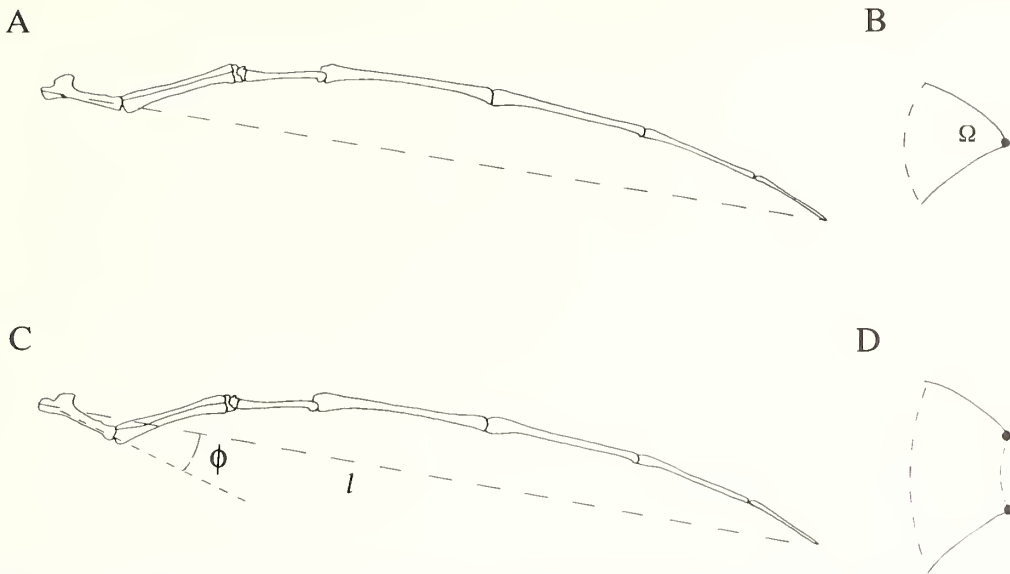
TEXT-FIG. 7. The effects of humeral rotation on the motion of the flight surface. A and C are based on Wellnhofer's reconstruction of the *Santanadactylus pricei* wing (1991, fig. 35). A, the humerus is held in the position of maximum extension (15° behind the transverse axis of the body), and the wingtip lies on the extension of the long axis of the humerus. The short dashed line represents the humeral long axis, about which the humerus rotates through angle θ, and the long dashed line joins wing root to wing tip (length l). B, pitch oscillation of the aerofoil produced by rotation of the humerus in the position of maximum extension (solid dot represents the position of the flight phalanx). C, the humerus is held in the position of maximum flexion (25° behind the transverse axis). D, the combination of pitch oscillation and vertical movement of the aerofoil, produced when the humerus is held in the position of maximum flexion. ϕ, the angle the long axis of the humerus is behind the line joining wing root to wing tip, which is approximately 15° behind the transverse axis.

hovering (or this form of pseudo-hovering) in *Santanadactylus brasilensis* is considered unlikely because hovering is prohibitively energetically expensive for flying vertebrates of moderate size, and becomes even more energetically expensive at larger sizes.

(ii) Pitch oscillation associated with no vertical movement of the wingtip has been observed in landing albatrosses and gannets (in wandering albatross *Diomedea exulans* it has a frequency of 5·1–5·8 Hz; Scholey 1982). It seems to form a braking manoeuvre. The rapidly alternating vortices on the pitching wing could increase induced drag in order to reduce forward speed; the need to continue to support the weight as speed decreases means that this mechanism is appropriate only for animals with high aspect ratio (Rayner 1986). It is possible that *Santanadactylus brasilensis*, and other similar pterosaurs, could have used pitching movements in similar situations.

Rapid pitch oscillation of the aerofoil is known from a number of other cases; it is thought to generate a bound vortex on the wing rapidly, and the movement relative to the body sheds this vortex into the air (Weis-Fogh 1973). However, without dorso-ventral movement of the wing

banthensis, DSB 759; 23, *Rhamphorhynchus longicaudus*, BMNH 37002; 24, *Pterodactylus* sp., BMNH R1776. Examples 1–17 are pterodactyloids, 18–23 are rhamphorhynchoids, and 24 is of unknown affinity. All specimens given with a museum were measured from the specimen, and those followed by a reference were measured from illustrations. AMNH, American Museum of Natural History; BMNH, British Museum (Natural History) London; BSP, Bayerisches Staatssammlung für Paläontologie und historisches Geologie, München; DSB, Petrefaktensammlung Kloster Banz.

relative to the body, it is unclear how the vortices shed into the air can provide thrust, although they may support the weight. One possible mechanism, which has not hitherto been recognized, and which has not been analysed theoretically, is that under wing rotation a medial portion of the wing will move dorso-ventrally, even though the wingtip may be almost stationary, provided that the leading edge of the wing is curved. This is the case in pterodactyloids (Wellnhofer 1985, 1991), as well as in many long-winged birds, and can be seen in the region of the elbow and hand in albatrosses in pitch oscillation. It is potentially possible that a small amount of useful thrust could be generated from this portion of the wing. This somewhat improbable hypothesis apart, we consider it unlikely that *Santanadactylus brasilensis* could use pitch oscillation alone to provide the thrust and weight support necessary for cruising flight.

If the humerus were folded back to 25° behind the transverse axis, ϕ would be 10°, and the wingtip would lie in front of the axis of the humerus; humeral rotation would therefore be partly converted into a vertical motion. If the humerus rotated through 70°, the aerofoil would undergo a pitch oscillation (Ω) of 68·8°; vertical excursion of the wingtip (h) would be 0·33 m, and the wingtip would move in a vertical arc of amplitude $\Phi = 11·4°$ (Text-fig. 7D).

The vertical movement and rotation combined could potentially provide useful lift and thrust for cruising flight. Assuming that *Santanadactylus pricei* was geometrically similar to Bramwell and Whitfield's (1974) reconstruction of *Pteranodon* (a mass of 2·56 kg, a wing area of 1·12 m² for a flight membrane not connecting to the leg, and a span of 3·27 m), calculations by using Rayner's (1986) model of the wake vortices appropriate for a long-winged bird indicate that there would be a small deficit of $-1·53$ N between the force needed for maintaining horizontal flight and the force produced by flapping the wing at an amplitude of 11°. This should be compared with a weight of 25·1 N, and total drag in level flight estimated at 3–4 N. The deficit force needed for horizontal flight could have been balanced by soaring. The best glide angle with the wings held static is 3·4°, and with the contribution made by the low amplitude wingbeat the best glide angle is reduced to 0·39°. The low amplitude wingbeat could therefore enable the use of weaker air movements to maintain horizontal flight. One of the reasons why this significant reduction in glide angle is possible is the size dependence of wingbeat amplitude in birds (Rayner 1988a); size-scaling of aerodynamic drag, and an increase in aspect ratio with mass imply that larger, longer-winged birds can fly with relatively lower wingbeat amplitudes. If this trend continues beyond the size range of extant birds, larger pterodactyloids may have obtained useful force from small amplitude wingbeats, which would not be aerodynamically helpful for smaller birds. This may explain the difference in dorsal excursion of the humerus between *Anhanguera santanae* (wingspan 4·1 m; Wellnhofer 1991) and the larger *Santanadactylus brasilensis* (wingspan 4·7 m): the latter species may have obtained sufficient force from wingbeats of much smaller amplitude. Nonetheless, the calculations above indicate that *Santanadactylus brasilensis* was not able to generate all the thrust required for level flight.

The musculature responsible for the rotation of the humerus about its long axis is not envisaged to be very different from that postulated by Padian (1983a), who proposed that the downstroke was produced by contraction of the pectoralis muscle, which originates on the sternum and attaches to the deltopectoral crest. Because the deltopectoral crest projects away from the shaft, contraction of the pectoralis will generate a turning moment tending to pronate the humerus, i.e. rotate the humerus forwards. This movement is necessary to drive pitching oscillations of the wing, and also to control angle of attack in relatively slow flight (Rayner 1988b). It is possible that – as in many birds (Goslow *et al.* 1989) – the pectoralis was functionally divided, with one component originating on the sternum responsible for pronation, and a second component originating below the humeral joint responsible for flapping.

Padian interpreted the supracoracoideus as acting as the principal antagonistic muscle to the pectoralis, bringing the humerus dorsally. Presumably, as in long-winged birds (Rayner 1988b), this muscle would have little function in cruising flight. However, its attachment on the dorsal surface of the humerus close to the shaft axis would mean that contraction will not supinate the humerus, i.e. rotate it posteriorly. Supination (the antagonist to the pectoralis during pitch oscillations) could be produced by a muscle ventral to the shoulder connecting to the medial crest (i.e. posterior to the

long axis of the humerus). A possible homologue to this muscle exists in the birds: the coracobrachialis caudalis. Wellnhofer (1991) has identified a process on the dorsal side of the scapular portion of the scapulocoracoid of *Santanadactylus brasilensis* which may have been the origin of a retractor, or more likely a supinator, muscle. Although the supracoracoideus is not envisaged to have played an important part in bringing about humeral rotation, it may have still had a rôle in stabilizing the humeral joint.

CONCLUSIONS

Certain Cretaceous pterodactyloids were not capable of the wing movements used by birds, bats and many other pterosaur species. The wing movements they could attain were not sufficient for them to maintain horizontal flight, but could form a useful aerodynamic contribution when soaring conditions were unfavourable; they could also be used in braking manoeuvres. Why should an animal evolve a mechanism which seems to have restricted flying ability? There are no obvious solutions to this problem. For such a restricted range of movement to have evolved, vertical movement of the wing must become redundant. This is only possible if favourable soaring conditions were always available, and if the animal could take off without producing additional force through flapping the wings. These are plausible conditions. Bramwell and Whitfield (1974) and Brower (1983) proposed that the conditions for thermal soaring were better in the Cretaceous than they are today because of the calm and warm conditions (Bowen 1966), with reduced latitudinal variation (Frakes 1979). Brower (1983) estimated that the useful range of soaring speeds for *Pteranodon* and *Nyctosaurus* were sufficient to enable them to soar into the seasonally average head wind encountered. Bramwell and Whitfield (1974) estimated that, because of its low wing loading, *Pteranodon* would have been capable of taking-off by simply spreading its wings into a head wind of speed in the region of 7 m s^{-1}. Alternatively, dropping into air deflected upwards by a cliff face would be a feasible method for initiating soaring without flapping, and this technique is used commonly by many large birds such as condors or albatrosses. The evolutionary pressure responsible for restricting the vertical movement of the humerus may have been the need to minimize wing inertia, and this pressure becomes more significant in larger species with longer wings. Although these pressures were presumably experienced by all long-winged pterosaurs, only a proportion of these forms actually evolved the restricted motion. Other species may have evolved other (unrecognized) means to reduce wing inertia, or may have used modes of flight, predation or habitat use which required them to retain the capacity for a full wingbeat, although they may not have been capable energetically of sustained flapping flight.

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G. A. HAZLEHURST

J. M. V. RAYNER

Department of Zoology
University of Bristol
Woodland Road
Bristol BS8 1UG, UK